HABITAT SELECTION AND SITE FIDELITY OF CANADA WARBLERS (*WILSONIA CANADENSIS*) IN CENTRAL NEW HAMPSHIRE

Michael Hallworth,[1,3] Amy Ueland,[1] Erik Anderson,[1]
J. Daniel Lambert,[2,4] and Leonard Reitsma[1]

[1]*Department of Biological Sciences, Plymouth State University, Plymouth, New Hampshire 03264, USA; and*
[2]*Conservation Biology Department, Vermont Institute of Natural Science, Quechee, Vermont 05059, USA*

Abstract.—Habitat selection by migratory bird species affects their fitness. Studies of populations with marked individuals of known reproductive performance provide the greatest insight on the relationship between a species and the range of habitats it occupies. Canada Warblers (*Wilsonia canadensis*) have not been intensively investigated at the population level, despite significant regional declines in their numbers over the past 40 years (e.g., 4.6% year^{-1} in New Hampshire). We mapped 92 male territories over four years and quantified habitat structure and habitat composition for territories and nonterritory areas. Analyses revealed more shrubs (stems and foliage), more perch trees, and lower canopy height on territories. Birds returned at an average rate of 52.0 ± 2.96% (SE) and exhibited average between-year shifts of 32 m in territory locations. Over the four years, males had high pairing success (91.0 ± 5.61%). Three-quarters of paired males fledged at least one young. Pairing and fledging success did not influence site fidelity. Paired males had more shrub stems and song-perch trees. Territories of earlier-arriving males had more shrub stems. The high proportion of males pairing and successfully fledging young, together with the high average return rates, indicate that areas with dense subcanopy vegetation constitute prime Canada Warbler breeding habitat in New Hampshire. Timber harvest practices that result in high shrub density and residual standing trees, such as deferment or two-age harvest, have the potential to slow Canada Warbler population declines, but only if they are widely applied in forest management. *Received 2 July 2007, accepted 21 March 2008.*

Key words: Canada Warbler, fledging success, habitat selection, pairing success, site fidelity, territories, *Wilsonia canadensis.*

Selección de Hábitat y Fidelidad a los Sitios en *Wilsonia canadensis* en el Centro de New Hampshire

Resumen.— La selección de hábitat por parte de especies migratorias de aves afecta su adecuación biológica. Los estudios de poblaciones con individuos marcados y de desempeño reproductivo conocido proveen los datos más informativos acerca de la relación entre una especie y el espectro de ambientes que ocupa. La especie *Wilsonia canadensis* no ha sido investigada a nivel de poblaciones de forma intensiva, a pesar de las disminuciones regionales significativas en sus números que han sucedido a lo largo de los últimos 40 años (e.g. 4.6% por año en New Hampshire). En este estudio construimos mapas de la ubicación de 92 territorios de machos a lo largo de cuatro años y cuantificamos la estructura y composición del hábitat para áreas con territorios y sin territorios. Los análisis indicaron que los territorios presentan más arbustos (tallos y follaje), más árboles de percha y menor altura del dosel. Las aves regresaron a una tasa promedio del 52.0 ± 2.96% (EE) y la ubicación de los territorios varió 32 m en promedio entre años. A lo largo de los cuatro años, los machos presentaron un éxito de apareamiento alto (91.0 ± 5.61%). Tres cuartas partes de los machos que tenían pareja produjeron por lo menos un volantón. El éxito de apareamiento y emplumamiento no influenció la fidelidad a los sitios. Los territorios de los machos apareados presentaron más tallos de arbustos y árboles de percha, y los de los machos que arribaron más temprano presentaron más tallos de arbustos. La alta proporción de machos que lograron conseguir pareja y criar exitosamente, junto con las altas tasas de retorno, indican que las áreas con cobertura densa de vegetación en el subdosel representan un hábitat óptimo para *W. canadensis* en New Hampshire. Las prácticas de extracción de madera que conducen a una alta densidad de arbustos y árboles residuales en pie, como el aplazamiento o la extracción de dos edades, tienen el potencial de desacelerar la disminución de las poblaciones de *W. canadensis*, pero sólo si son aplicadas ampliamente en el manejo de los bosques.

[3]E-mail: m_hallworth@yahoo.com
[4]Present address: American Bird Conservancy, Vermont Center for Ecostudies, Norwich, Vermont 05055, USA.

IN RECENT DECADES, a major focus of bird ecology has been the analysis of habitat selection, in part because it strongly influences avian distribution, abundance, and reproductive success. Individuals use specific habitat cues that may occur in different vegetation community types (Wilson et al. 1998). Certain structural components are known to be necessary to meet species-specific breeding requirements (Block et al. 1987). Territory selection by woodland birds occurs at several scales and combines the individual importance of various site-specific factors, including forest area and isolation, edge effects, social and demographic features of conspecifics, stand structure, and floristic composition (McCollin 1998). In particular, population studies have clearly shown that North American migratory warblers seek specific habitat features in selecting territory locations (Hunt 1996, Jones and Robertson 2001, Peters et al. 2005). Only through population studies with individuals of known reproductive performance can we understand the fitness consequences of both the habitat selected and the habitat used by a particular species (Jones 2001). Comparing occupied and unoccupied areas within structurally heterogeneous habitat provides insight regarding individual choices that lead to habitat selection. Monitoring reproductive success among individuals in a population over consecutive years allows direct measures of how the use of habitat influences individual fitness (Jones 2001). Intensive population studies can be of particular importance for species of conservation concern. Only through studies of habitat selection, reproductive success, and site fidelity can we detect variation in individual fitness and, hence, population dynamics.

Many migratory passerines exhibit high breeding-site fidelity, often for as long as they survive (e.g., Howlett and Stutchbury 2003). Return rates range widely among migratory warblers during the breeding season. Holmes and Sherry (1992) found that 39% of Black-throated Blue Warblers (*Dendroica caerulescens*) and 27% of American Redstarts (*Setophaga ruticilla*) returned to the same breeding site after the year of banding. Howlett and Stutchbury (2003) found that 48% of Hooded Warblers (*Wilsonia citrina*) breeding in Pennsylvania returned the year after banding. The Canada Warbler (*W. canadensis*), a small (10–12 g) Neotropical–Nearctic migrant, has a life history similar to that of the other species just mentioned, but it has not been intensively studied at the population level.

Across their breeding range, Canada Warblers inhabit several lowland and upland habitats, including swamps, streamside thickets, brushy ravines, moist forests, and regenerating timber cuts (Ellison 1984, Smith 1994, Conway 1999, Hallworth et al. 2008, Reitsma et al. 2008). They also occur on reforested talus slopes and in subalpine forests with adequate deciduous undergrowth (Sabo 1980). They forage among shrubs and primarily nest on the ground. They typically inhabit areas with dense shrub layers and a structurally complex forest floor with tussocky mounds and dense stems of forbs, ferns, and saplings. Two Canadian studies indicated an association with disturbed areas within older-growth forests (Schieck and Nietfeld 1995, Drapeau et al. 2000).

Community-level investigations have found Canada Warblers occurring at varying densities in several habitats. Highest natural densities occur in swamps and riparian forests, where wet conditions limit canopy closure and favor shrub growth (Swift et al. 1984, Robbins et al. 1989, LaRue et al. 1995, Miller 1999, Golet et al. 2001).

In a study in Maine of upland forest stands in various successional stages, Hagan et al. (1997) found that Canada Warblers were most abundant in harvested areas 6–20 years postcut. Canada Warblers use managed stands with high understory density (Hagan and Meehan 2002) and residual trees (Titterington et al. 1979). In New Hampshire, Canada Warblers occur in early- to midsuccessional forest stands and within the deciduous understory of mature forests, usually in association with canopy disturbance (DeGraaf et al. 1998, King and DeGraaf 2000).

The Breeding Bird Survey indicates that the Canada Warbler has been declining by 2.7% year^{-1} throughout its breeding range. In New Hampshire, the species has been declining by 4.6% year^{-1} since 1966 (Sauer et al. 2006). The species is listed as a Partners In Flight "continental watchlist species," and the North American Bird Conservation Initiative has designated this species as a highest-priority landbird in Conservation Region 14 (Atlantic Northern Forest) for both conservation and research (Dettmers 2003). Despite the declines, efforts to characterize the habitat requirements of this species have been limited, nearly all of the information coming from community-level census work rather than intensive population-level investigations (Lambert and Faccio 2005). We conducted an intensive population study of the Canada Warbler to examine the relationship between reproductive performance and habitat structure and to investigate whether site fidelity is associated with prior reproductive success and specific habitat attributes. We predicted that high shrub-stem and foliage densities and greater numbers of emergent trees suitable as song-perches are critical components to Canada Warblers, regardless of the species composition of the shrubs and trees, and that these structural features are more abundant on territories than on adjacent unoccupied habitat. We also predicted that reproductive success positively influences site fidelity.

METHODS

Study site.—The study was conducted in Canaan, New Hampshire (43°40'N, 72°03'W), on the Canaan Town Forest (40 ha) and the adjacent Bear Pond Natural Area (BPNA; 363 ha) (Fig. 1). Canaan is a rural town with >85% forest cover. It is surrounded by sparsely populated towns to the north, east, and south, each with even greater levels of forest cover. Large private holdings to the north and east link the study area to the White Mountain National Forest. The town to the west is more populated; however, forest is the primary land cover here as well.

The lower plot (Canaan Town Forest and southern BPNA) is a swamp dominated by Red Maple (*Acer rubrum*), Balsam Fir (*Abies balsamea*), and Red Spruce (*Picea rubens*), interspersed with mixed upland forest. The understory (2.50–7.99 cm diameter at breast height [DBH]) is dominated by Common Winterberry (*Ilex verticillata*), Mountain Holly (*I. montana*), and Balsam Fir (Ueland 2004), and the groundcover comprises mosses, ferns, grasses, and forbs (see Van de Poll [2006] for species list). The upper plot (all within BPNA) is separated from the lower plot by Bear Pond and its associated quaking bog. This plot is a mixed upland forest that was intensively harvested in 1985. The harvest removed >90% of the standing timber, the residual standing trees presumed to be of low commercial value. Areas with steeper slopes had lower harvest rates. The
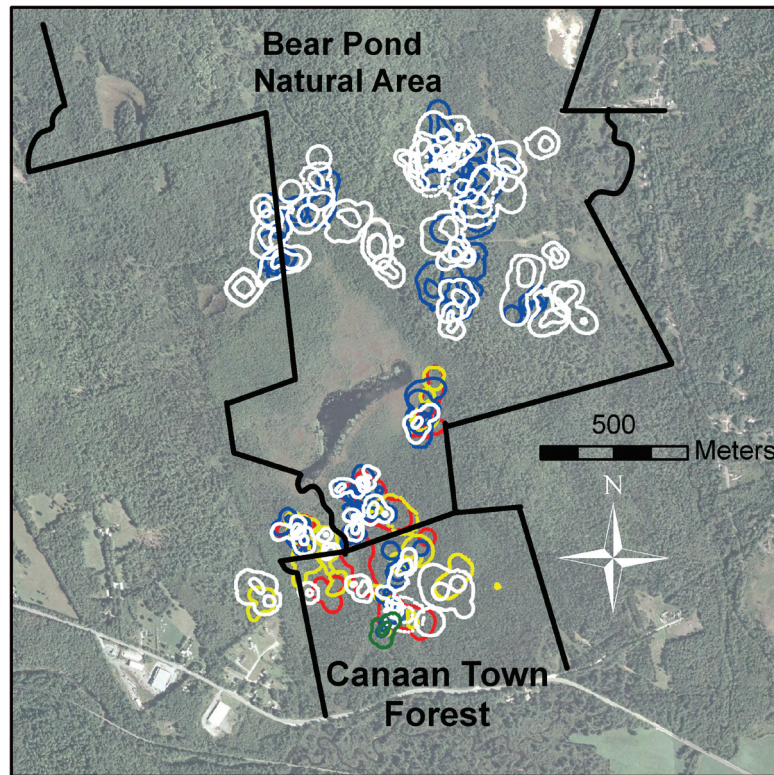
Fig. 1. Map of the study site in Canaan, New Hampshire, with male Canada Warbler territories overlaid. Male territories in 2003 are indicated in red, 2004 in yellow, 2005 in blue, and 2006 in white. Both territory (95% ADK, larger) and core area (50% ADK) are shown.

result was a clearcut with remnant trees, isolated or in clumps. The trees (≥8.0 cm DBH) in this area include a mix of Red Maple, Balsam Fir, Eastern Hemlock (*Tsuga canadensis*), Red Spruce, and Bigtooth Aspen (*Populus grandidentata*). Balsam Fir dominates the smallest size class of shrubs and saplings (<2.5 cm DBH), followed by a cohort of *Ilex* spp. and *Viburnum* spp., Paper Birch (*Betula papyrifera*), and Red Maple. The larger size class of shrubs and saplings (2.50–7.99 cm DBH) mainly comprises Balsam Fir, Paper Birch, Red Maple, and Quaking Aspen (*Populus tremuloides*). The average groundcover for ferns, moss, and grass is 20%, 14%, and 6%, respectively. Species of *Ilex* and *Viburnum* were combined into one category for analyses because of their structural similarity (Ueland 2004). Hallworth et al. (2008) provide additional details of the study area.

Characterizing male territories.—From 2003 to 2006, we captured territorial males in mist nets using audio playback. If a bird did not respond to the recorded Canada Warbler song, that individual was recorded and his song was used as a playback. We used a carved decoy in 2005 and 2006. All birds were marked with unique color-band combinations. Ninety-three percent (66 of 71) of territorial males were banded throughout the study. Unbanded individuals were surrounded by marked males, making it possible to map their territories. We aged birds according to their plumage characteristics (Rappole 1983, Pyle 1997). We mapped male territories from 26 May to 9 July, 2003–2006. We observed territorial males for two 30-min periods in each of three

consecutive 15-day observation periods but never followed a marked bird on consecutive days. During each observation period, we recorded the bird's location at 5-min intervals with a Garmin 72 or 76 global positioning system (GPS). This resulted in a total of six 30-min observation bouts and a minimum of 42 data points for each mapped territorial male. We recorded locations only after birds moved to new perches, so as not to influence movement. We recorded the same point on multiple occasions when there was no movement for ≥10 min. All territory mapping was conducted between dawn and 0930 hours EDT.

We documented pairing and fledging success for each male within these observation bouts. A male was considered paired if one of the following was observed: a female was repeatedly detected within the territory beyond the early phase of female assessment, or an active nest was found within a territory (Bayne and Hobson 2001). We considered territorial males unpaired if they sang from high perches throughout the breeding season and no female was seen or heard within the territory. We considered a nest successful if at least one fledgling was seen in the territory (Howlett and Stutchbury 2003) or if males and females delivered food to multiple areas within the territory.

We used the adaptive kernel (ADK) method to delineate the territory boundaries (95% ADK) and the "core" territory areas (50% ADK) of each individual (Barg et al. 2005). We calculated territory boundaries and sizes using the CALHOME home-range analysis program (Kie et al. 1994).

Site fidelity.—We calculated the average territory movements for returning males among years using ARCMAP, version 9.1 (ESRI, Redlands, California). For each returning male, we measured the distance from the farthest point of the territory in each cardinal direction to the corresponding point of the previous year's territory. We employed this method for both the territory (95% ADK) and the core area (50% ADK). All measurements were averaged to obtain the territory movement from the previous year. If an individual had more than one core area, we averaged all possible combinations. There were no individuals that had multiple core areas one year and only a single core area the next. If an individual had one core area one year and two core areas the next, we measured the distances from the single core area to the two core areas and then averaged them.

Vegetation sampling.—We used a modification of the Breeding Biology Research and Monitoring (BBIRD) protocol (Martin and Conway 1994) to quantify all vegetation characteristics. Only males from 2005 and 2006 with the full set of six complete observation bouts were used in habitat analyses (*n* = 39). We located these 39 sets of vegetation plots, each consisting of four 11.3-m-radius subplots (0.04 ha), within minimum convex polygons (MCPs) that encompassed all observation points within a territory. Having started with this protocol in 2003, we used MCPs to maintain consistency in locating sampling plots across all years. We placed the first subplot at the polygon's center, with each peripheral subplot located at bearings of 0°, 120°, and 240° from the center. If a subplot contained fewer than two observations of territorial males or was >50% outside of the polygon, we shifted it the least distance possible, so that (1) it did not overlap with another subplot, (2) it remained >50% within the polygon, and (3) it included the maximum possible number of observations of the territorial male. We used fewer than four subplots in territories that were too small to accommodate that number without overlap; 24 territories had all four subplots, 13 territories had three, 1 territory had two, and 1 territory had one.

We established 32 nonterritory vegetation plots within surveyed habitat not occupied by Canada Warblers using a random-number generator to create coordinates. We then overlaid those coordinates onto a map of the study site and placed every 20th coordinate on this map. If the selected coordinate fell outside of an existing territory, we considered it a central nonterritory vegetation subplot and positioned the three peripheral subplots accordingly, making sure that no subplots were on territories.

We quantified the number of potential song-perch trees in each vegetation subplot. We based our designation of song-perch trees on the degree of isolation and visibility of a tree that emerged from the subcanopy and on observations of singing males in trees with these attributes. A potential song-perch tree was any tree that emerged ≥3 m above the surrounding canopy and was surrounded by a gap measuring ≥5 m in breadth. These perch trees provide high visibility during singing and maximize the distance at which a song can be heard by conspecifics. Mosses, grasses, and ferns were the only groundcover categories quantified, because in preliminary analyses these were the only significant variables between occupied and unoccupied areas (Ueland 2004, Anderson 2005). We quantified the foliar density of the shrub strata using a pole (2.5 m long and 2.5 cm in diameter) marked at 0.5-m intervals. Within each 0.5-m interval, we recorded the plant species and the

number of times its branch or leaf touched the pole. We placed the pole 1 m from the center of the plot in each of the four cardinal directions. For analysis, we averaged the four subplots of each set for each territory or nonterritory analogue to best approximate the habitat in the area sampled.

Statistical analyses.—We used only males with a complete set of six 30-min observation bouts to compare pairing and fledging success, and we used only the subset of these males from both 2005 and 2006 for vegetation analyses. All statistical analyses were conducted using SPSS, version 14.0 (SPSS, Chicago, Illinois). We employed an information-theoretic approach to construct models for the habitat-selection analysis (Burnham and Anderson 2001). We chose 11 biologically relevant variables on the basis of personal observations and 4 variables on the basis of previous studies for analysis (Ueland 2004, Anderson 2005). The variables included the sum of all shrub-stems (sumshrub: >1 m in height, <8.0 cm DBH,) within a 5-m radius, number of small shrub-stems (<2.5: >1 m in height, <2.5 cm DBH) within a 5-m radius, number of large shrub-stems (>2.5: >1 m in height, 2.50–7.99 cm DBH; Ueland 2004, Anderson 2005) within a 5-m radius, average canopy height (canhgt) within 0.04 ha (11.3-m radius), sum of coniferous (conif) and deciduous (decid) trees within an 11.3-m radius, number of small snags (smsnag: 8–23 cm DBH; Anderson 2005) within an 11.3-m radius, sum of all snags (sumsnag) within an 11.3-m radius, number of perch trees (perch) within an 11.3-m radius, percent cover of three groundcover types (fern, grass, and moss; Ueland 2004) within a 5-m radius, and three shrub-strata density measurements (shrubstrat3: 1.0–1.5 m; shrubstrat4: 1.5–2.0 m; shrubstrat5: 2.0–2.5 m). We calculated binary logistic regressions (presence or absence of Canada Warblers) in SPSS. Kullback-Leibler information and Akaike's information criterion (AIC), corrected for small sample sizes (AIC$_c$; Burnham and Anderson 2001), were used to evaluate the models. The lowest ΔAIC value indicates the model that best balances goodness-of-fit with minimizing the number of parameters in the model.

In subsequent AIC analyses that examined arrival time of males, level of site fidelity (high site fidelity = returning ≤25 m from the previous year's territory; low site fidelity = returning >25 m from the previous year's territory), pairing success, and fledging success, we used the six variables (sumshrub, perch, <2.5, >2.5, shrubstrat5, and canhgt) from models in the habitat-selection analysis with ΔAIC values <4.0. Models that have a ΔAIC value ≤2.0 have substantial support, whereas those ≥4.0 and ≤7.0 have less support but may offer useful insight into observed patterns (Burnham and Anderson 2001).

We used Fisher's exact test to determine whether site fidelity was influenced by the previous year's pairing or fledging success. Analysis of variance was used to analyze differences in territory and core area sizes among years and to compare the distance of male territory shifts among years. We used α = 0.05 for all statistical tests. All results are stated as means ± SE.

Results

Ninety-two male territories had complete sets of six 30-min observation bouts over the four years of the study (Fig. 1): 76 territories of after-second-year (ASY) males, 14 territories of second-year (SY) males, and two territories of males of unknown age.

TABLE 1. Territory sizes and core areas (± SE) of male Canada Warblers in each year, calculated by adaptive kernel analysis. Ranges of both territories and core areas are also given for each year. These data are based exclusively on males for which a full set of location data points were obtained ($n = 92$). Only the core areas in 2004 were significantly different from those in other years. Territories did not differ significantly.

Year	Territory		Core	
	Size	Range	Size	Range
2003	1.12 ± 0.24	2.57–0.43	0.19 ± 0.07	0.63–0.06
2004	0.70 ± 0.14	2.16–0.15	0.11 ± 0.02	0.23–0.02
2005	1.17 ± 0.15	3.36–0.29	0.19 ± 0.03	0.77–0.03
2006	1.24 ± 0.12	3.33–0.26	0.24 ± 0.02	0.67–0.03

Male territories.—The mean territory size (95% ADK) for all four years was 0.968 ± 0.980 ha (Table 1). There was no significant difference in territory size between years ($F = 1.71$, df = 3, $P = 0.17$). The mean core area (50% ADK) for all four years was 0.169 ± 0.021 ha. In 2004, the core area was significantly smaller than in 2003, 2005, and 2006 ($F = 2.82$, df = 3, $P = 0.044$).

Habitat selection.—The sum of all shrub-stems (>1 m in height and <8.0 cm DBH) provided the best model for habitat selection in Canada Warblers (Table 2). The model including high density of shrubs, low canopy height, high foliage density in the vertical layer 2.0–2.5 m, and number of perch trees within a territory also had parsimony with respect to the habitat selected by Canada Warblers ($\Delta AIC_c = 0.04$). The variables that were included

TABLE 2. Vegetation characteristics measured and analyzed as part of our Canada Warbler study in west-central New Hampshire. These characteristics were analyzed using Kullback-Leibler information, and Akaike's information criterion (AIC), corrected for small sample sizes (AIC_c) was used to evaluate the models (Burnham and Anderson 2001). The lowest ΔAIC_c value indicates the model that best balances goodness-of-fit with minimizing the number of parameters in the model. The results clearly document the significance of shrub-stem densities for Canada Warblers (see text for greater detail in each vegetation category). W_i indicates the ranked model weights, and k is the number of variables included in the model. See text for definitions of variables.

Model	AIC_c	ΔAIC_c	W_i	k
sumshrub	71.821	0.000	0.381	1
shrubstrat 5, perch, canhgt, sumshrub	71.859	0.038	0.374	4
sumshrub, perch, canhgt	73.862	2.040	0.137	3
<2.5, >2.5	75.551	3.729	0.059	2
<2.5, >2.5, canhgt, perch	77.620	5.799	0.021	4
perch, canhgt, sumsnag, sumshrub	77.901	6.080	0.018	4
smsnag, <2.5, >2.5	79.507	7.235	0.010	3
fern, grass, moss, <2.5, >2.5	87.895	16.073	0.000	5
conif, decide, shrubstrat3, shrubstrat4, shrubstrat5	97.358	25.536	0.000	5
global	104.303	32.481	0.000	15

TABLE 3. Variable importance weights (ΣW_i) for the six variables (see text) that were included in the models with ΔAIC_c values <4.00. Importance of explanatory variables was assessed by summing all candidate model weights that included that variable (Burnham and Anderson 2001). Values closer to 1.00 indicate higher importance compared with other variables in the candidate model set. The highest variable importance weight in each analysis is in bold.

Variable	ΣW_i				
	Habitat selection	Arrival time	Site fidelity	Pairing success	Fledging success
sumshrub	**0.91**	**0.93**	**0.59**	0.41	0.69
<2.5	0.09	0.06	0.10	0.09	**0.96**
>2.5	0.09	0.06	0.10	0.15	**0.96**
shrubstrat5	0.37	0.12	0.12	0.31	0.74
canhgt	0.55	0.06	0.31	0.06	0.65
perch	0.55	0.39	0.43	**0.83**	0.68

in the models with $\Delta AIC_c < 4.00$ were sum of all shrub-stems, number of shrub-stems <2.5 cm DBH, number of shrub stems >2.5 cm DBH, foliage density between 2.0 and 2.5 m, canopy height, and number of song-perch trees. The variable importance weights for these six variables are 0.91, 0.09, 0.09, 0.37, 0.55, and 0.55, respectively (Table 3).

The most parsimonious model for male arrival time was the sum of all shrubs (variable importance weight [ΣW_i] = 0.93; Tables 3 and 4). Males that arrived earlier (within the first week of the breeding season) had greater shrub-stem densities (earlier males = 48.96 ± 2.39 stems/5-m radius; later males = 39.74 ± 2.20 stems/5-m radius). An additional simple model includes the sum of all shrubs and the number of song-perch trees ($\Delta AIC_c = 2.12$).

Reproductive success.—The percentage of males paired in 2003, 2004, 2005, and 2006 was 90% (9 of 10), 85% (11 of 13), 92% (22 of 24), and 93% (42 of 45), respectively. Of the males that paired successfully, 75% (63 of 84) fledged at least one young: 78% (7 of 9) in 2003, 72% (8 of 11) in 2004, 77% (17 of 22) in 2005, and 74% (31 of 42) in 2006 fledged at least one young. The overall pairing rate was 91% (84 of 92).

The number of song-perch trees ($\Sigma W_i = 0.83$) constituted the most important variable in the simplest model for male pairing success (see Tables 3 and 5). This model was closely followed by

TABLE 4. Habitat analysis, using Akaike's information criterion (AIC), relating male arrival time to the six habitat variables (see text) that had the most support in the habitat analysis. Both the sum of all shrubs and the number of song-perch trees were included in the most parsimonious models.

Model	AIC_c	ΔAIC_c	W_i	k
sumshrub	27.67	0.00	0.555	1
perch, sumshrub	29.79	2.12	0.192	2
shrubstrat5, perch, sumshrub	30.76	3.09	0.118	3
canhgt, perch, sumshrub	32.05	4.38	0.062	3
<2.5, >2.5	32.19	4.53	0.058	2
perch	35.11	7.44	0.013	1
global	38.88	11.22	0.002	6

TABLE 5. Akaike's information criterion (AIC) was used to explain the habitat variables (see text) associated with male pairing success. Number of song-perch trees and the sum of all shrubs were included in the most parsimonious models.

Model	AIC_c	ΔAIC_c	W_i	k
perch	32.14	0.00	0.434	1
perch, sumshrub	33.80	1.66	0.189	2
perch, >2.5, shrubstrat5	34.28	2.14	0.149	3
<2.5, sumshrub, shrubstrat5	35.22	3.07	0.093	3
perch, sumshrub, shrubstrat5	36.01	3.87	0.063	3
canhgt, perch, sumshrub	36.04	3.90	0.062	3
global	39.62	7.48	0.010	6

TABLE 6. Akaike's information criterion (AIC) was used to determine the habitat variables that influence fledging success. The global model that included all six habitat variables was the most parsimonious model. Numbers of shrubs of the small (<2.5) and large (>2.5) size classess were included in the next-best model.

Model	AIC_c	ΔAIC_c	W_i	k
global	52.64	0.00	0.649	6
<2.5, >2.5	54.17	2.06	0.232	2
<2.5, >2.5, shrubstrat5	56.84	4.20	0.080	3
perch, sumshrub	58.93	6.29	0.028	2
sumshrub, shrubstrat5	61.77	9.12	0.007	2
sumshrub	63.30	10.66	0.003	1
canhgt, sumshrub, shrubstrat5	64.02	11.38	0.002	3

the number of song-perch trees and the sum of all shrub-stems ($\Delta AIC_c = 1.66$). For males that successfully fledged at least one young, the model with the greatest parsimony included all six variables (Table 6); however, one additional model that included shrubs of both the large and small size classes was also parsimonious ($\Delta AIC_c = 2.06$, $\Sigma W_i = 0.96$ for both shrub size classes; Table 3). Paired males successfully fledging at least one young had greater total shrub densities (average for successful males = 42.98 ± 2.16, average for unsuccessful males = 40.34 ± 2.42) and higher shrub densities <2.5 cm DBH (successful = 36.48 ± 2.51, unsuccessful = 25.0 ± 2.47).

Site fidelity.—The return rates for territorial males in 2003–2004, 2004–2005, and 2005–2006 were 57%, 50%, and 47%, respectively. The average return rate for all four years was 52%. Twenty-five percent of males banded in 2003 returned in 2005, and 10% of birds banded in 2003 returned in all three years. The mean territory shifts for all males over the three years 2003–2004, 2004–2005, and 2005–2006 were 27.6 ± 5.4 m, 36.9 ± 11.2 m, and 31.1 ± 6.5 m, respectively. There was no significant difference among years ($F = 0.29$, df = 2, $P = 0.75$).

The two most parsimonious models with respect to site fidelity contained either the sum of all shrubs or the number of perch trees and sum of all shrubs combined (Table 7). The variable importance weight (ΣW_i) of the sum of all shrubs was 0.59, and that of the number of song-perch trees was 0.43 (Table 2). We also found that the distance by which a male's territory shifted (≤ 25 m or >25 m) was not influenced by either the pairing success (Fisher's exact test: $P = 0.579$) or the fledging success (Fisher's exact test: $P = 0.604$) of the previous year.

DISCUSSION

We found that Canada Warblers selected areas with high shrub densities and emergent trees. Compared with nonterritory locations, territories contained denser shrub foliage between 2.0 and 2.5 m above ground, lower canopies, and higher numbers of perch sites. Two studies conducted in upland forests of New Hampshire and Wisconsin found that Canada Warblers concentrate their feeding effort in shrubs and low tree branches at heights of 3–5 m (Sabo and Holmes 1983, Sodhi and Paszkowski 1995). This range corresponds to the leafy stratum often formed by wetland shrubs, much like the shrub thickets in poorly drained areas of the lower

TABLE 7. Akaike's information criterion (AIC) was used to determine habitat variables associated with male site fidelity. The sum of all shrubs, the number of song-perch trees, and the average canopy height were included in the most parsimonious models.

Model	AIC_c	ΔAIC_c	W_i	k
sumshrub	22.71	0.00	0.371	1
perch, canhgt	23.05	0.34	0.313	2
<2.5, >2.5	25.34	2.62	0.100	2
perch, sumshrub	25.37	2.66	0.098	2
shrubstrat5, sumshrub	25.38	2.67	0.098	2
shrubstart5, sumshrub, perch	28.55	5.84	0.020	3
global	40.33	17.62	0.000	6

and upper plots in the present study. Sodhi and Paszkowski (1995) found that the mean foraging height of male Canada Warblers in early-successional forests was 4.06 ± 0.25 m and that they forage as low as 0.3 m, and that female mean foraging height was 3.07 ± 0.27 m and that they forage as low as 1 m. Robbins et al. (1989) found a positive relationship between abundance of Canada Warblers and foliage density between 0.3 and 1 m. The high foliar density of the shrub layer from 2.0 to 2.5 m within territories in the present study provides ample substrate for foraging and cover, especially in the vicinity of nests (M. Hallworth et al. pers. obs.).

The importance of song-perch trees in attracting females is clearly indicated by our analysis. Also, females appear to select males whose territories contain high densities of shrubs. All of the habitat variables that emerged as the most important in our habitat-selection analysis appear to also play a role in males' success in fledging young. In particular, stem densities of both small and large shrubs are likely to provide the necessary concealment for young fledglings.

Earlier-arriving males settled into habitat with higher shrub-stems than those that arrived later. The difference in timing of arrival (>80% of territorial males on site within 10 days of the earliest to settle) is much less than in other species that migrate shorter distances, yet this difference may have habitat-selection consequences. The advantages of dense shrub foliage are apparent, because leafy understories may contribute to reproductive success through concealment of nests and fledglings.

Site fidelity was influenced by the total number of shrub-stems on a male's territory, the number of perch trees, and the canopy height, whereas neither pairing nor fledging success in the previous year influenced male territory shifts. Presumably, the concealment provided by high numbers of shrub-stems and the availability of conspicuous song-perch trees attract males to the same locations year after year. Canopy height may also serve to increase the visibility of song-perch sites, thereby increasing the probability of early and successful pairing. We could not compare returning males with nonreturning males, because we did not know whether a nonreturning male had dispersed off the study site or died.

In a related study of the same population (Hallworth et al. 2008), we found no differences between the second-growth plot and the Red Maple swamp in overall stem density, number of song-perches, and canopy height. However, fine-scale features differed and, together with the fact that individual males in the Red Maple swamp used 40–50% less area, this suggests that the swamp is higher-quality habitat. The important differences include twice the number of small deciduous stems and more moss in the swamp. These differences did not influence site fidelity or the proportion of males fledging at least one young, which were relatively high on both plots. So, despite differences in certain details of habitat structure, reproductive performance was not affected.

We also found that older males had territories with lower canopy heights than first-year males (Reitsma et al. 2008). Older males also had more song-perch trees and higher total shrub-stem densities on the second-growth plot, which underscores the influence of these habitat features on habitat selection.

In the present study, the Red Maple swamp (lower plot) was a level expanse comprising deciduous swamp thickets interspersed with coniferous trees growing in better-drained soils. The second-growth (upper) plot has greater topographic relief, with a central drainage covered in thick, short stems of deciduous and coniferous species. The proximity of the swamp to the upper plot, and the central drainage of the upper plot itself, may play a role in attracting Canada Warblers to this younger forest. Males on both plots exhibit site fidelity toward both poorly drained and well-drained forested stands. Over the four years of the present study, the earliest-arriving males were within the denser stands with more persistent standing water, but success at pairing and fledging young did not differ among males on the two study plots despite plot-scale differences in habitat structure. Canada Warblers may select habitat partly on the basis of social cuing (Doligez et al. 2002). If so, the total number of males in our study area may have depended, in part, on the richer "hotspots" that, in turn, attract additional singing males to neighboring early-succession stands with similarly dense, short stems. More work is needed to determine whether social cuing influences the total number of pairs in the study area.

The return rates in the present study are among the highest published for all Neotropical migrants (e.g., Holmes and Sherry 1992, Howlett and Stutchbury 2003). These high return rates and site fidelity, together with the high rate of pairing and fledging success, indicate that the study area includes high-quality breeding habitat for this regionally declining species. Because Canada Warblers successfully breed in areas with high numbers of shrub stems and emergent trees, conservation of Red Maple swamps and clearcutting with residual tree retention are two strategies that could reverse the decline of this species in the northeastern United States. Forest managers and land-use planners have not given due consideration to the ecological significance of Red Maple swamps. Failure to recognize the value of this habitat to vulnerable species such as Canada Warbler has led to its drainage and conversion to marketable timber stands or developed land.

Forestry management strategies such as two-age or deferment harvests that leave mature trees among intensive cuts are often based more on economics than on intentional benefit to wildlife. For example, the retention of many Red Maples on the upper plot in the present study is likely attributable to the lower profitability of this species, but the benefit to Canada Warblers is potentially significant. Relatively heavy harvests that leave commercially low-value song-perch trees such as Red Maple could result in greater availability of the type of habitat selected by Canada Warblers. More research is needed to determine whether Canada Warblers are habitat-limited in the northeastern United States. As migrants, their problems may lie elsewhere. Conversion of mature forest to earlier-succession stands may have consequences for mature-forest birds; therefore, landscape-level targets for such conversion must be part of a comprehensive management strategy for multiple species.

LITERATURE CITED

ANDERSON, E. A. 2005. Habitat characteristics of paired and unpaired male Canada Warblers (*Wilsonia canadensis*) in a forested wetland in Canaan, NH. M.Ed. thesis, Plymouth State University, Plymouth, New Hampshire.

BARG, J. J., J. JONES, AND R. J. ROBERTSON. 2005. Describing breeding territories of migratory passerines: Suggestions for sampling, choice of estimator, and delineation of core areas. Journal of Animal Ecology 74:139–149.

BAYNE, E. M., AND K. A. HOBSON. 2001. Effects of habitat fragmentation on pairing success of Ovenbirds: Importance of male age and floater behavior. Auk 118:380–388.

BLOCK, W. M., K. A. WITH, AND M. L. MORRISON. 1987. On measuring bird habitat: Influence of observer variability and sample size. Condor 89:241–251.

BURNHAM, K. P., AND D. R. ANDERSON. 2001. Kullback-Leibler information as a basis for strong inference in ecological studies. Wildlife Research 28:111–119.

CONWAY, C. J. 1999. Canada Warbler (*Wilsonia canadensis*). *In* The Birds of North America, no. 421 (A. Poole and F. Gill, Eds.). Academy of Natural Sciences, Philadelphia, and American Ornithologists' Union, Washington, D.C.

DEGRAAF, R. M., J. B. HESTBECK, AND M. YAMASAKI. 1998. Associations between breeding bird abundance and stand structure in the White Mountains, New Hampshire and Maine, USA. Forest Ecology and Management 103:217–233.

DETTMERS, R. 2003. Priority Bird Species in Bird Conservation Region 14. North American Bird Conservation Initiative, Arlington, Virginia.

DOLIGEZ, B., E. DANCHIN, AND J. CLOBERT. 2002. Public information and breeding habitat selection in a wild bird population. Science 297:1168–1170.

DRAPEAU, P., A. LEDUC, J.-F. GIROUX, J.-P. L. SAVARD, Y. BERGERON, AND W. L. VICKERY. 2000. Landscape-scale disturbances and changes in bird communities of boreal mixed-wood forests. Ecological Monographs 70:423–444.

ELLISON, W. G. 1984. Canada Warbler (*Wilsonia canadensis*). Pages 326–327 *in* The Atlas of Breeding Birds of Vermont (S. B. Laughlin and D. P. Kibbe, Eds.). University Press of New England, Hanover, New Hampshire.

GOLET, F. C., Y. WANG, J. S. MERROW, AND W. R. DERAGON. 2001. Relationships between habitat and landscape features and the avian community of Red Maple swamps in southern Rhode Island. Wilson Bulletin 113:217–227.

HAGAN, J. M., P. S. MCKINLEY, A. L. MEEHAN, AND S. L. GROVE. 1997. Diversity and abundance of landbirds in a northeastern industrial forest. Journal of Wildlife Management 61:718–735.

HAGAN, J. M., AND A. L. MEEHAN. 2002. The effectiveness of stand-level and landscape-level variables for explaining bird occurrence in an industrial forest. Forest Science 48:231–242.

HALLWORTH, M., P. M. BENHAM, J. D. LAMBERT, AND L. REITSMA. 2008. Canada Warbler (*Wilsonia canadensis*) breeding ecology in young forest stands compared to Red Maple (*Acer rubrum*) swamp. Forest Ecology and Management 255:1353–1358.

HOLMES, R. T., AND T. W. SHERRY. 1992. Site fidelity of migratory warblers in temperate breeding and Neotropical wintering areas: Implications for population dynamics, habitat selection, and conservation. Pages 563–575 *in* Ecology and Conservation of Neotropical Migrant Landbirds (J. M. Hagan III and D. W. Johnston, Eds.). Smithsonian Institution Press, Washington, D.C.

HOWLETT, J. S., AND B. J. M. STUTCHBURY. 2003. Determinants of between-season site, territory, and mate fidelity in Hooded Warblers (*Wilsonia citrina*). Auk 120:457–465.

HUNT, P. D. 1996. Habitat selection by American Redstarts along a successional gradient in northern hardwoods forest: Evaluation of habitat quality. Auk 113:875–888.

JONES, J. 2001. Habitat selection studies in avian ecology: A critical review. Auk 118:557–562.

JONES, J., AND R. J. ROBERTSON. 2001. Territory and nest-site selection of Cerulean Warblers in Eastern Ontario. Auk 118:727–735.

KIE, J. G., J. A. BALDWIN, AND C. J. EVANS. 1994. CALHOME home range analysis program. U.S. Forest Service, Pacific Southwest Research Station, and California Department of Fish and Game, Fresno.

KING, D. I., AND R. M. DEGRAAF. 2000. Bird species diversity and nesting success in mature, clearcut and shelterwood forest in northern New Hampshire, USA. Forest Ecology and Management 129:227–235.

LAMBERT, J. D., AND S. D. FACCIO. 2005. Canada Warbler Population Status, Habitat Use, and Stewardship Guidelines for Northeastern Forests. VINS Technical Report 05-4, Quechee, Vermont.

LARUE, P., L. BÉLANGER, AND J. HUOT. 1995. Riparian edge effects on boreal Balsam Fir bird communities. Canadian Journal of Forest Research 25:555–566.

MARTIN, T. E., AND C. J. CONWAY. 1994. BBIRD Field Protocol. Montana Cooperative Wildlife Research Unit, University of Montana, Missoula.

MCCOLLIN, D. 1998. Forest edges and habitat selection in birds: A functional approach. Ecography 21:247–260.

MILLER, N. A. 1999. Landscape and habitat predictors of Canada Warbler (*Wilsonia canadensis*) and Northern Waterthrush (*Seiurus noveboracensis*) occurrence in Rhode Island swamps. M.S. thesis, University of Rhode Island, Kingston.

PETERS, K. A., R. A. LANCIA, AND J. A. GERWIN. 2005. Swainson's Warbler habitat selection in a managed bottomland hardwood forest. Journal of Wildlife Management 69:409–417.

PYLE, P. 1997. Identification Guide to North American Birds, part I: Columbidae to Ploceidae. Slate Creek Press, Bolinas, California.

RAPPOLE, J. H. 1983. Analysis of plumage variation in the Canada Warbler. Journal of Field Ornithology 54:152–159.

REITSMA, L. R., M. T. HALLWORTH, AND P. M. BENHAM. 2008. Does age influence territory size, habitat selection, and reproductive success of male Canada Warblers in central New Hampshire? Wilson Journal of Ornithology 120:446–454.

ROBBINS, C. S., D. K. DAWSON, AND B. A. DOWELL. 1989. Habitat area requirements of breeding forest birds of the middle Atlantic states. Wildlife Monographs, no. 103.

SABO, S. R. 1980. Niche and habitat relations in subalpine bird communities of the White Mountains of New Hampshire. Ecological Monographs 50:241–259.

SABO, S. R., AND R. T. HOLMES. 1983. Foraging niches and the structure of forest bird communities in contrasting montane habitats. Condor 85:121–138.

SAUER, J. R., J. E. HINES, AND J. FALLON. 2006. The North American Breeding Bird Survey, Results and Analysis 1966–2006, version 6.2.2006. U.S. Geological Survey Patuxent Wildlife Research Center, Laurel, Maryland.

SCHIECK, J., AND M. NIETFELD. 1995. Bird species richness and abundance in relation to stand age and structure in aspen mixedwood forests in Alberta. Pages 115–157 *in* Relationships between Stand Age, Stand Structure, and Biodiversity in Aspen Mixedwood Forests in Alberta (J. B. Stelfox, Ed.). Alberta Environmental Centre, Vegreville, and Canadian Forest Service, Edmonton, Alberta.

SMITH, S. 1994. Canada Warbler (*Wilsonia canadensis*). Page 302 *in* Atlas of Breeding Birds of New Hampshire (C. Foss, Ed.). Chalford, Dover, New Hampshire.

SODHI, N. S., AND C. A. PASZKOWSKI. 1995. Habitat use and foraging behavior of four parulid warblers in a second-growth forest. Journal of Field Ornithology 66:277–288.

SWIFT, B. L., J. S. LARSON, AND R. M. DEGRAAF. 1984. Relationship of breeding bird density and diversity to habitat variables in forested wetlands. Wilson Bulletin 96:48–59.

Titterington, R. W., H. S. Crawford, and B. N. Burgason. 1979. Songbird responses to commercial clear-cutting in Maine spruce–fir forests. Journal of Wildlife Management 43:602–609.

Ueland, A. 2004. Habitat selection of Canada Warblers in a forested wetland in Canaan NH. M.Ed. thesis, Plymouth State University, Plymouth, New Hampshire.

Van de Poll, R. 2006. Final report on a partial natural resources inventory of the Bear Pond Natural Area. Pages 8–38 *in* Natural Resource Inventory of the Bear Pond Natural Area 2003–2005 (L. Reitsma, Ed.). Canaan, New Hampshire.

Wilson, W. H., Jr., R. E. Zierzow, and A. R. Savage. 1998. Habitat selection by peatland birds in a central Maine bog: The effects of scale and year. Journal of Field Ornithology 69:540–548.

Associate Editor: J. Jones